507.73
P4P6842

ISSN 0097-4463

ANNALS
of CARNEGIE MUSEUM

CARNEGIE MUSEUM OF NATURAL HISTORY

4400 FORBES AVENUE • PITTSBURGH, PENNSYLVANIA 15213
VOLUME 51 2 JULY 1982 ARTICLE 12

FOSSIL SMALL MAMMALS FROM THE KECHABTA FORMATION, NORTHWESTERN TUNISIA

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Abstract

Small collections of fossil mammals from several localities in the Kechabta Formation of northwestern Tunisia contain insectivores, lagomorphs, and rodents. These taxa support a late Vallesian to mid-Turolian age for the Kechabta Formation. One new species of Cricetidae, *Zramys jaegeri,* is described.

Introduction

Since 1967, the University of Colorado Museum has coordinated a multinational program to collect and study the fossil vertebrates from the Neogene rocks of Tunisia. The earlier part of the program concentrated on the larger vertebrates from the Beglia Formation (Middle Miocene) of central Tunisia. Since 1971, fossil smaller vertebrates of Middle and Late Miocene age and some of Pliocene age have been collected from a number of sites in northern Tunisia. The oldest of these localities is in the Middle Miocene part of the Hakima Formation

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Submitted 11 February 1982.

(Robinson and Black, 1973). The purpose of the present paper is to describe the fossil smaller mammals from the Upper Miocene Kechabta Formation in the area from Jendouba (Souk el Arba) to south of El Kef, northwestern Tunisia. Comments on fossils from the Hakima Formation supplement an earlier paper (Robinson and Black, 1973). The geology and Cricetidae are reported by Robinson, the Muridae and Sciuridae by Black, the Erinaceidae and Soricidae by Krishtalka, and the Ochotonidae by Dawson. These fossils help to date the Hakima and Kechabta Formations, complement Jaeger's (1977*b*) study of Maghreb Miocene rodents, and add information on the smaller mammals of the Middle and Late Miocene of the Maghreb. Collections from the younger Mellegue Group in northern Tunisia will be described later.

ABBREVIATIONS

T-, 0000 field numbers of specimens in the SGT; L, length; W, width; SGT—Service Géologique de Tunisie; UCM—University of Colorado Museum; CM—Carnegie Museum of Natural History. (All measurements are in millimeters.)

GEOLOGIC SETTING

The post-Burdigalian continental deposits of Tunisia north of the Dorsale are found in a number of more or less isolated basins related to tectonically complex situations. The numerous diapirs of the region have been active for a long time; very few of the outcrops are not involved in this diapirism. Biely et al. (1974) established a stratigraphic framework for the region based in part on the work of Burollet (1951). They proposed that the lower sequence be called the Medjerda Group including, from base to top, the Hakima, Oued Melah, Kechabta, and Oued bel Khedim Formations of Burollet (1951). This group is predominantly continental in origin and often contains very coarse conglomerates. Brackish water beds may occur in the Oued bel Khedim and Oued Melah Formations, especially in the northeast. They also proposed the Mellegue Group, containing the Tessa (lower) and Oued Djouama (upper) Formations; where contacts are visible, the Mellegue Group unconformably overlies the Medjerda Group. The only localities where these contacts are not angular and can be observed are at Araguib Kammra, southeast of El Kef (Burollet, 1956), and in the valley of the Oued Mellegue, south of Jendouba.

Correlation of the deposits in the El Kef-Jendouba area with those of the type sections of the Hakima-Kechabta Formations south of Bizerte is difficult; however, the superb section at the Araguib Kammra cited by Burollet (1956) resembles the latter. Fossils have been recovered from all of these formations.

PREVIOUS WORK

The first Neogene locality in northern Tunisia that produced a fossil vertebrate fauna was Lac Ichkeul (Arambourg and Arnould, 1949; Jaeger, 1971; Coppens, 1971), where both large and small mammals were collected. This locality is possibly in the Oued Djouama Formation. Undescribed material subsequently collected includes: a jaw of a juvenile individual of *Hipparion* sp. from the Hakima Formation near Ben Mtir dam, north of Jendouba; a complete skull of *Hipparion* sp. from the Oued Melah Formation southeast of Mateur at Kef en Nsoura; and two *Hipparion* teeth from near the base of the Kechabta Formation at Oued Mellegue (Biely et al., 1974). All of this material is in the collections of the SGT.

Described material subsequently collected includes: mastodont and rodent remains from Djebel Semmene in the Kechabta Formation northeast of Jendouba (Jaeger, 1977*b*; Bergounioux and Crouzel, 1956); a small collection from the Hakima Formation near Testour (Robinson and Black, 1973). The results of this previous work indicated that the Hakima Formation was late Astaracian to Vallesian, the Kechabta, Vallesian and Turolian, and the Djouama, at least in part, Villafranchian.

NEW LOCALITIES

New localities found since 1971 are:

Hakima Formation.—At Testour, slightly higher in the section then the locality reported by Robinson and Black (1973).

Kechabta Formation.—1) Voie Ferrée: on the west bank of the Oued Mellegue, some 12 km south of Jendouba near the top of the formation (40 m west of an abandoned railway bed). 2) MDM locality, Zag et Tir: an exposure southwest of El Kef near the Marabout of Sidi Ounis, near the section cited by Burollet (1956), and slightly below the freshwater limestones at the top of the section. 3) Araguib Kammra: in a ravine exposed west of the El Kef-Sbeitla road, 9–10 km southeast of El Kef. This section, about 4 km west of that cited by Burollet (1956), contains several localities, including one near the contact of the Kechabta and the Oued bel Khedim Formations.

Tessa Formation.—1) Koudiat er Rouabi: 34 km east of El Kef and 1.5 km north of the road. Two levels are productive here: one is approximately 50 m above the base of the exposures that have a faulted lower contact; the second level was 10–12 m above the first, but has been destroyed by recent construction. 2) Calcaires Lacustres: 33 km east of El Kef and 5 km south of the road. The productive bed is a dark organic shale in a sequence containing freshwater limestones. It is 45–50 m above the contact with folded Eocene limestones. 3) An exposure on the top of a hill, 5 km south of Hammam Biada, and east of Oued Tessa.

AGE OF THE HAKIMA FORMATION

The first vertebrate specimen from the Testour localities in the Hakima Formation was discovered in samples being sorted for foraminifera. More intensive collecting produced the faunule described by Robinson and Black (1973). These deposits were thought to represent a sequence of continuous marine sedimentation from the Oligocene to the Late Miocene (Bajanik and Salaj, 1971), even though such a sequence had never been found in northern Africa, a region where the Burdigalian marine sediments lie unconformably upon older sediments. Robinson and Black (1974) accepted the foraminiferal evidence. Their 1974 paper was prepared for and presented at the 75th anniversary meeting of the Egyptian Geological Survey in 1971. Later, Robinson and Black (1973) considered the foraminifera to have been reworked and that the mammalian fauna indicated a true late Miocene age. Recent field work by Professor M. B. Cita of the University of Milan has confirmed (written communication to Robinson, 1976) the reworked nature of the sediments; the mammalian fauna definitely indicates a late Astaracian (middle Serravallian) age for these deposits, not an Aquitanian or Burdigalian one.

The four beds in the Hakima Formation, Testour area, that produced bone were designated localities 00, 0, 1, 2, from oldest to youngest. The fauna from one of these, locality 00, has been described (Robinson and Black, 1973). Localities 0–2 occur in one section on the north side of Djebel Ras el Krab, in a location where the base of the Hakima Formation is in fault contact with a diapir of Triassic rock. At locality 00, about 1 km to the west of localities 0–2, the same diapir does not intersect the Hakima Formation, but is in fault contact with the upper (continental) part of the Oligocene Fortuna Sandstone; here the Hakima Formation overlies the Fortuna Sandstone unconformably. Locality 00 is some 5 m above the contact with the Fortuna Sandstone. Although stratigraphically higher, the exact positions of localities 0–2 relative to 00 cannot be determined; there are no discernable differences among the taxa from these localities.

LOCALITIES IN THE KECHABTA FORMATION

The Kechabta Formation is extensively exposed from southeast of Bizerte (type section at Djebel Kechabta, Burrollet, 1951) to west of the Algerian frontier. It is usually in tectonically complex situations due to the numerous diapirs in the region and to at least two phases of post-Kechabta orogeny. The sections at the Oued Mellegue, Testour, and Araguib Kammra preserve the stratigraphic relationships of the Kechabta to the underlying Hakima Formation. At the Araguib Kammra, the upper shale unit of the Medjerda Group, the Oued bel Khedim Formation, is preserved (Burollet, 1956). At this exposure, the unconformity between the Medjerda and Mellegue groups is less pronounced than elsewhere. The locality of Voie Ferrée, at Oued Mellegue, is near the top of the preserved Kechabta sequence, but the overlying Tessa Formation rests upon the Kechabta with a pronounced angular unconformity indicating significant erosion of the Kechabta prior to deposition of the Tessa Formation.

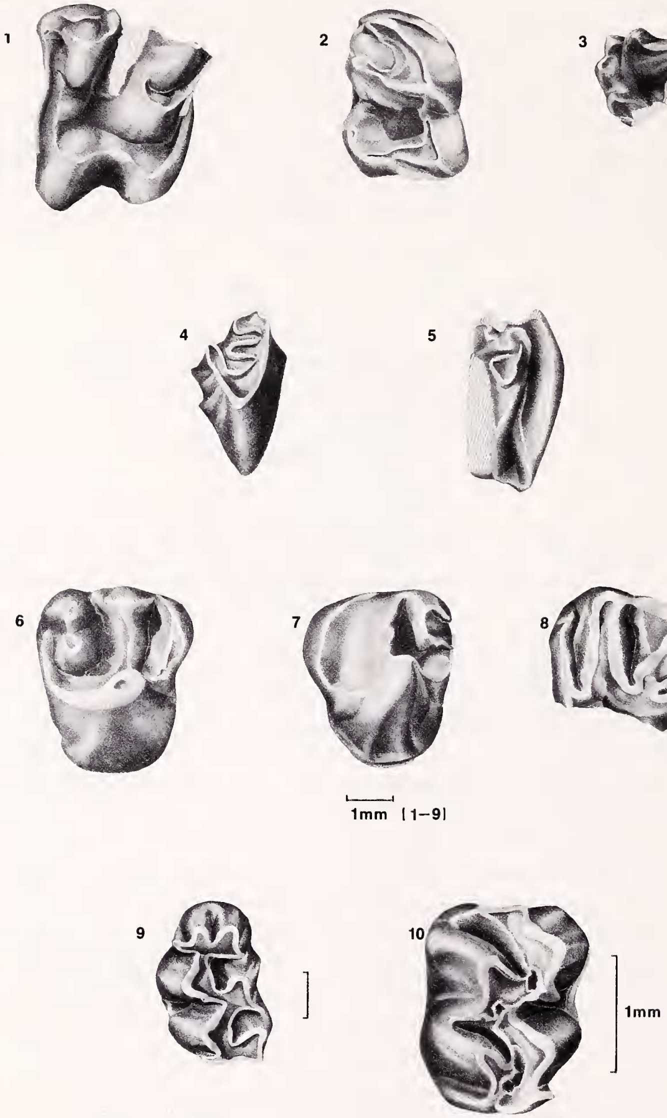
SYSTEMATIC ACCOUNTS

Order Insectivora Illiger, 1811
Family Erinaceidae Fischer von Waldheim, 1817
Schizogalerix Engesser, 1980
Schizogalerix moedlingensis (Rabeder), 1973
Schizogalerix ?moedlingensis
Figs. 1, 2

Referred specimens.—T-4421, isolated left M^1; T-4417, fragment of right dentary with M_2, roots of M_3; T-4423, isolated left M_2.

Locality.—UCM locality 77290, MDM locality, Zag et Tir: Turolian.

Description.—The posterolabial border is broken away from the isolated M^1 ($L = 2.6+$; $W = 3.4$). The crown is quadrate in occlusal view with essentially straight anterior and posterior margins and a deep lingual emargination. The M^1 bears six major cusps aligned labiolingually in two high, parallel rows; the protocone, paraconule, and paracone form the anterior row; the hypocone, metaconule, and metacone, the posterior one. In occlusal view, the apices of the paraconule and metaconule are anterior, respectively, to imaginary lines connecting the apices of the protocone and paracone, and the metacone and hypocone. A deep valley separates the two rows of cusps and extends lingually from the buccal border of the crown to a high crest that unites the protocone and hypocone. Apart from the paraconule, all of the major cusps are subcrescentic, with high convex lingual faces and concave labial ones, so that their apices point bucally. The protocone, the largest of the cusps, occupies the anterolingual corner of the crown. The preprotocrista is short, parallel to the anterior margin of the tooth, and extends to the small, low, pyramidal paraconule. The postprotocrista runs posteriorly and joins the prehypocrista to form a high crest that demarcates the lingual and occlusal surfaces of the crown. The base of the protocone extends farther lingually than that of the hypocone, creating a deep emargination between the two cusps on the lingual surface of the crown. The hypocone is lower and less compressed anteroposteriorly than the protocone. A small cuspule occurs between the two cusps at the junction of the prehypocrista and postprotocrista. The posthypocrista runs labially for a short distance and ends at the base of the crown at a point directly posterior to the metaconule. The latter, about four times as large as the paraconule, is higher than the hypocone, but lower than the metacone. The premetaconulecrista is short, but the longer postmetaconulecrista runs posterolabially to form a broad metacingulum along the posterior wall of the metacone. The latter is the highest cusp on the crown. The premetacrista is short and appears to become thicker (?mesostyle) at its broken labial edge. The paracone also bears a short preparacrista and a longer postparacrista that ends in a large mesostyle. Importantly, the latter is not connected posteriorly to any crests. If, as it appears, two mesostyles were present,



Figs. 1, 2.—*Schizogalerix ?moedlingensis*. 1) T-4421, left M^1. 2) T-4417, right M$_2$.
Fig. 3.—Soricidae indet. T-4312, left P^4.
Figs. 4, 5.—*Prolagus* sp. 4) T-3807, P^2. 5) T-3806, P^4.
Figs. 6–8.—*Atlantoxerus* sp. 6) T-4403, right M^1 or M^2. 7) T-4344, left P^4. 8) T-4313, left M^1 or M^2.
Figs. 9, 10.—*Zramys jaegeri*, new species. 9) T-4419, left M^1, holotype. 10) T-4407, right M^2.

they would have been completely separate on an unbroken M^1. A low conical parastyle occurs directly anterior to the apex of the paracone, and is separated by a notch from the preparacrista. The precingulum is strong and runs lingually from the parastyle to the anterior part of the base of the protocone. The postcingulum is short and weak, as is the parastylar ectocingulum.

T-4417 is a jaw fragment with a slightly worn M_2 (L = 2.5; W = 2.0) and the roots of a much smaller M_3. T-4423, another M_2 (L = 2.6; W = 2.2), is highly worn. The lower molars lean lingually, so that the labial face of the crown is long and sloping. The trigonid and talonid are equal in length, but the latter extends farther buccally than the trigonid. In occlusal view, the crown of M_2 is essentially rectangular, except for the anterolingual orientation of the anterior face of the trigonid. The posterior wall of the trigonid is also oriented anterolingually, so that the metaconid occurs more anteriorly, relative to the protoconid. The paraconid, an elongate cusp, is connected to the protoconid by a broadly worn paracristid, but is isolated from the higher, conical metaconid. The anterior cingulid is strong, but does not extend onto the buccal surface of the crown. The talonid bears two main cusps—a broad, low hypoconid, and a higher entoconid that is laterally compressed and drawn out toward the metaconid. As is typical of erinaceids, the cristid obliqua meets the trigonid wall labially, below the worn apex of the protoconid, and is parallel to the long axis of the tooth. As a result, the hypoflexid notch is very shallow. On the opposite side of the crown, a small notch separates the bases of the metaconid and entoconid, and, in lingual view, this notch is at the same height as that between the paraconid and metaconid. The posterior border of the talonid is parallel to that of the trigonid, and shows no evidence of a hypoconulid. Rather, two crests meet at the midpoint of the posterior margin of the talonid basin: a short hypocristid and a longer postcingulid that runs obliquely from the tip of the entoconid to the posterolabial part of the base of the talonid.

Discussion.—Schizogalerix, a new genus of echinosoricine erinaceid, was named by Engesser (1980) for a number of new species from the Miocene of Turkey and North Africa, as well as some formerly included in *Galerix* [*S. moedlingensis, S. voesendorfensis, S. zapfei* (including *S. attica*)]. Species that Engesser (1980) retained in *Galerix* are the generotype, *G. exilis,* and *G. socialis*. Accordingly, the insectivore material recently described from the Turolian of Samos (Black et al., 1980) belongs to *S. zapfei* (=*S. attica*) rather than *G. atticus*.

Among the characters preserved on the three molars described here, *Schizogalerix* differs from *Galerix,* according to Engesser (1980), in the presence of a divided mesostyle and an isolated metaconule on M^1, and, on M_2, in the tendency to develop a "free-ended" hypocristid. Some of these features may not, however, be consistently diagnostic. Upper molars of *Galerix socialis* (Engesser, 1972:45, Fig. 1; 48, Fig. 3) also have an isolated metaconule and the lower molars (Engesser, 1972:46, Fig. 2) do not differ from those of many species assigned to *Schizogalerix* (Engesser, 1980:64, Fig. 3) in the structure of the hypocristid-postcingulid complex.

The M^1 described here appears to have had the divided mesostyle characteristic of *Schizogalerix*. The M_2s are referred to the same taxon as the M^1 on the basis of association and similar size. All three teeth most closely resemble comparable parts of the dentition of *S. moed-*

lingensis, among described species of that genus—the anterior mesostyle on M^1 appears to have been completely separated from the premetacrista and, if present, the posterior mesostyle; the hypocristid-postcingulid junction is medial and strong (Engesser, 1980:74, Fig. 11). However, referral of these teeth to *S. moedlingensis* is tentative, because of the small sample size, the missing and potentially diagnostic metastylar area of M^1, and the variable occurrence of some of the above mentioned features in material assigned to *S.* aff. *voesendorfensis* and a number of new species of *Schizogalerix* (Engesser, 1980: Figs. 3a, 3e, 4c, 10, 14, 19c). The size of the teeth is also not helpful taxonomically. According to Engesser's (1980:71,72) data, described species of *Schizogalerix* have closely overlapping ranges of variation in size of M^1 and M_2. The material discussed here is slightly larger than M^1 and M_2 of these species, and, if it does belong to *S. moedlingensis,* would increase the known range of variation in size of M^1 and M_2 of that species.

S. moedlingensis is otherwise known only from Eichkogel, an Austrian locality of late early Turolian age (Engesser, 1980).

Family Soricidae Gray, 1821
Soricid indet.
Fig. 3

Referred specimen.—T-4312, isolated left P^4.

Locality.—Voie Ferrée; Turolian

Description.—This fragmentary P^4 ($L = 1.7$; $W = 1.7+$) is missing the hypoconal shelf (posterolingual corner of the crown). The labial part of the crown is dominated by a high, conical paracone and a slightly lower crest that extends from the latter to the posterolabial tip of the crown. A strong lip of enamel runs lingually from this point and forms the posterior margin of the occlusal surface of the premolar. Curiously, a wide flange of enamel, of which the posterior margin is broken, extends posteriorly from the base of the crown along the entire preserved posterior margin of the tooth. This flange does not appear to have been part of the occlusal surface, but may have filled the interdental embrasure between P^4 and M^1. The preserved part of the lingual half of the crown bears a small protocone and hypocone, both of which occur on the anterior margin of the tooth. The protocone is very close to the small parastyle, whereas the hypocone is more lingual. The labiolingual orientation of the preserved part of the posterior margin of the hypoconal shelf implies that the posterior emargination in this area was only slight.

Discussion.—This isolated and fragmentary P^4 cannot be identified to subfamilial, much less generic, level. The proximity of the protocone to the parastyle and the slight posterior emargination are features that occur in a number of crocidurines and soricines.

Order Lagomorpha Brandt, 1855
Family Ochotonidae Thomas, 1897
Prolagus Pomel, 1853
***Prolagus* sp.**
Figs. 4, 5

Referred specimens.—T-3806, P^4; T-3807, P^2 (L = 1.0; W = 1.6); T-4240, P_3 (L = 1.7; W = 1.9).

Locality.—Voie Ferrée; Turolian.

Discussion.—The three teeth are referrable to a species of *Prolagus,* but the sample is too small to permit reference to any of the notably variable species of this genus. P^2 (Fig. 4) is a relatively advanced tooth with short external and medial lobes and a long internal lobe that extends buccally in front of the medial lobe. The tooth is thus more advanced than in *P. oeningensis* and resembles that of *P. michauxi* (Lopez-Martinez and Thaler, 1975) and some variants from Polgardi (Tobien, 1963), Kohfidisch (Bachmeyer and Wilson, 1970), and Pikermi (Lopez-Martinez, 1976). P^4, a broken specimen (Fig. 5) has traces of two buccal lakes. P_3 has the structure typical of *Prolagus* and lacks a crochet. This is the earliest record of *Prolagus* in Africa, predating the Villafranchian occurrences in Algeria and Tunisia (Michaux, 1975; Jaeger, 1971) and marking a break from the earlier faunas in which the lagomorphs are represented by *Kenyalagomys* and its allies.

Order Rodentia Bowdich, 1821
Family Sciuridae Gray, 1821
Genus *Atlantoxerus* Major, 1893
***Atlantoxerus* sp.**
Figs. 6, 7, 8

Referred specimens.—T-4344, LP^4 (L = 2.37, W = 2.80); T-4313, LM^1 or M^2 (W = 2.80); T-4403, RM^1 or M^2 (L = 2.37, W = 3.00).

Localities.—Voie Ferrée (T-4344); Araguib Kammra B (T-4313); MDM locality, Zag et Tir (T-4403). All Turolian.

Description.—P^4 has a wide anterior cingulum, with a high parastyle. The protoloph is a high, thin crest with only a slight wrinkle at the posterior margin of the protoconule. The metaconule is isolated from the protocone and has a thin crest passing posteroanteriorly a short way along the posterior margin of the tooth.

The upper molars display rather narrow anterior basins with moderate parastyles. The protolophs are narrow, without protoconules. The metalophs are short, terminate in large metaconules, and are separate from the protocones except in a very advanced stage of wear. The posterior arm of the protocone ends behind the metaloph between the metacone and metaconule.

Discussion.—The three specimens are clearly those of *Atlantoxerus* but the material is much too fragmentary for a specific assignment.

Table 1.—*Measurements (in mm) of undamaged specimens of* Zramys jaegeri.

T. no.	Tooth	Length	Width
4419	M^1	2.50	1.68
4418	M^1	2.62	1.81
4415	M^1	2.92	1.84
4414	M^2	2.00	1.45
4407	M^2	1.95	1.57
4410	M^3	1.35	1.45
4406	M_1	2.40	1.52
4405	M_1	2.47	1.48
4408	M_2	1.92	1.49
4413	M_2	2.08	1.62
4424	M_2	2.00	1.50
4422	M_2	2.21	1.65

Family Cricetidae Rochbrunne, 1883
Subfamily Uncertain
Genus ***Zramys*** Jaeger and Michaux, 1973, *in* Jaeger et al., 1973
***Zramys jaegeri*,** new species
Figs. 9, 10; Table 1

Holotype.—T-4419, M^1.

Hypodigm.—T-4420, M^1–M^2 eroded; T-4419 (holotype), 4418, 4415, M^1; T-4407, 4411, 4412, 4414, M^2; T-4410, M^3; T-4405, 4406, 4416, M_1; T-4404, 4408, 4413, 4414, 4422, M_2.

Locality.—UCM Locality 77290; MDM Locality, near Sidi Ounis, Zag et Tir, southwest of El Kef, Tunisia. Turolian.

Diagnosis.—Size of *Z. dubius* and *Z. semmemensis*; M_1 with well developed posterior ectoloph, anterocone deeply cleft and usually with anterbuccal and anterolingual spurs directed laterally but not as extreme as in *Z. haichai*; posterior ectoloph at buccal margin of tooth not forming partial spur ending lingual to the buccal margin as in *Z. semmemensis* and *Z. haichai*.

Description.—Although teeth other than M^1 are known, only the M^1 of *Z. semmemensis* was figured by Jaeger (1977*b*); no other comparative material is described in the literature. *Z. jaegeri* is more hypsodont than *Z. semmemensis* and the closure of the posterior fold (terminology of Van de Weerd, 1976) indicates a more derived condition than in the species from Djebel Semmene. One specimen (T-4418) is lacking the anterolingual spur but has the well developed posterior ectoloph and anterobuccal spur.

Discussion.—There is confusion about the subfamilial status of *Zramys*. Jaeger (1977*b*) placed it in "subfamily indet." (p. 87), but suggested (p. 109) that it is closely related to *Mellalomys atlasi,* which he (1977*a,* 1977*b*) placed in the Myocricetodontinae. He also stated that *Zramys* may have given rise to a form from Lac Ichkeul which resembles *Ruscinomys*. Lavocat (1961) did not include *Cricetodon atlasi* (now *Mellalomys atlasi*) within the Myocricetodontinae, but compared it to *Cricetodon gregarius hispanicus*. *Cricetodon gregarius* has now been made the type of a new genus, *Megacricetodon,* and the subspecies *hispanicus* has been elevated to a species of *Megacricetodon* (Mein and Freudenthal, 1971).

One of the important characteristics of the tribe Cricetodontini is the presence of four to five roots on the M^1, whereas the Megacricetodontini, *Zramys,* and *Mellalomys,* all have three. One of the characteristics of the Myocricetodontinae (if *Mellalomys* is excluded) is the presence of a prominent accessory lingual cusp on M^1. Although Jaeger's (1977*b*) classification is followed here, more detailed studies may support including the *Mellalomys-Zramys* group within an uncertain tribe of the Cricetodontinae. *Megacricetodon* often has a spur (eperon) behind the paracone of M^1 as does *Zramys* (Mein and Freudenthal, 1971:23).

De Bruijn (1976) and Tobien (1978) placed *Byzantinia* and *Turkomys* in the tribe Cricetodontini. Although the number of the roots of M^1 of these genera is not given by Tobien, two specimens of *Byzantinia hellenicus,* CM-36258 and CM-36260, each have four roots. If this character is constant, the *Turkomys-Byzantinia* lineage is more closely related to *Hispanomys-Ruscinomys* than either is to the *Mellalomys-Zramys* group.

In the *Hispanomys-Ruscinomys* lineage, there is a gradual development of hypsodonty, a tendency for the completion of the ectoloph, and a simplification of pattern (Van de Weerd, 1976). These genera do not have a lingual anterolophule spur on M^1. In the *Turkomys-Byzantinia* lineage the anterolophule spur becomes well developed (Freudenthal, 1970: Fig. 1; De Bruijn, 1976: pl. 1, Fig. 5, 8; Tobien, 1978: Fig. 10; Black et al., 1980: Fig. 7c). The presence of an anterolophule spur and a complete ectoloph in *Hispanomys sofcaensis* (Tobien, 1978), suggest that it should probably be placed in *Byzantinia* (as Unay, 1980:402, has done). The position of *H. eskihisarensis* is problematical as it lacks the anterolophule spur but has an elongate M^3 characteristic of *Turkomys-Byzantinia*. In *Turkomys pasalarensis* and *T. candirensis* the spur is weak, and perhaps some individuals did not develop it. Unay's (1980) discussion of the diverse *Byzantinia* material from Bayraktepe helps to fill in details of the lineage.

In *Zramys,* a functionally similar but not homologous crest is present in some species, including the type, *Z. haichai* (Jaeger, 1977*b*: pl. 4, Fig. 1, 2). This crest, here termed the anterolingual spur, projects from the posterior part of the lingual portion of the anterocone, and may be accompanied by an anterobuccal spur on the buccal portion of the anterocone. In *Zramys,* the development of the ectoloph is not as pronounced as in either *Ruscinomys* or *Byzantinia*. However, in *Zramys,* there is no tendency for the simplification of pattern found in *Ruscinomys*. The complex pattern of the M^1 of *Zramys* is matched by the M_1 (Jaeger, 1977*b*: pl. 4, Fig. 5), which is much more complex than M_1 of *Byzantinia* (Black et al., 1980: Fig. 7a) or *Ruscinomys* (Van de Weerd, 1976: pl. 13, Fig. 1).

The *Hispanomys-Ruscinomys* lineage seems to have been restricted to southwest Europe (with the possible exception of *H. eskihisarensis,* although Unay, 1980, may be right in placing this species in *Byzantinia*), the *Turkomys-Byzantinia* lineage to southeast Europe and Anatolia, and *Zramys* to northwest Africa (De Bruijn, 1976:367). Throughout the Middle and Late Miocene there appear to have been at least three centers of cricetodontine evolution in which a general tendency for hypsodonty, marked bilobation of the anterocone of M^1 and development of an ectoloph occurred. The hypsodonty became extreme in Ruscinian *Ruscinomys*; Ruscinian *Zramys* and *Byzantinia* are not known.

Subfamily Myocricetodontinae Lavocat, 1961
Genus ***Myocricetodon*** Lavocat, 1961
Myocricetodon seboui Jaeger, 1977*b*
Myocricetodon* sp. cf. *M. seboui

Referred specimen.—T-4396. Left M^1, missing anterocone.

Locality.—Araguib Kammra C, approximately 50 m below AK-B and approximately 60 m below the contact with the Oued bel Khedim Formation. Turolian or latest Vallesian.

Discussion.—This is the only known cricetid specimen from the Araguib Kammra. The lack of the anterocone makes certain identification doubtful, but the M^1 possesses the cusp behind the protocone typical of most *Myocricetodon*; the width of M^1, 0.85 mm, is well within the range of size given by Jaeger (1977*b*) for *M. seboui* from Oued Zra. The geologic record of *M. seboui,* according to Jaeger (1977*b*), extends from middle Vallesian to late early or early middle Turolian. The specimens that Jaeger (1977*b*) reported from Djebel Semmene (*M.* sp. cf. *M. seboui*) were all larger than the sample of *M. seboui* from Oued Zra, as were those from Amama 2. The Araguib Kammra specimen is closest in size to M^1 of *M. seboui* from Oued Zra (late Vallesian).

Family Muridae Gray, 1821

There are two species of murids represented in the collections from the Kechabta Formation of north central Tunisia. These are of Turolian age and possibly contemporaneous with species from Amama 2 (Algeria) and Khendek el Ouaich (Morocco) (Jaeger, 1975).

Table 2.—*Measurements (in mm) of cheek teeth of species of* Anthracomys.

Species	M^1		M^2		M_1	
	L	W	L	W	L	W
Anthracomys majori (Michaux, 1971)	3.40	2.10	1.90	2.10	2.80	1.90
Anthracomys filfilae (Petter, 1968)	—	—	—	—	3.00	2.00
Anthracomys meini (Michaux, 1969)	2.42	1.65	—	—	2.12	1.34
Anthracomys anomalus (De Bruijn et al., 1970)	2.19	1.57	1.57	1.54	2.08	1.36
Anthracomys miocaenicus (Jaeger, 1975)	2.32	1.57	1.47	—	2.08	1.35
Anthracomys species A	2.10	1.40	1.40	1.35	—	—
Anthrocomys species B	2.80[a]	2.15[a]	2.10	2.00	2.50	1.60

[a] M^1 broken, measurement approximate.

Older murids are known from North Africa, with *Progonomys* cf. *P. cathalai* from Bou-Hanifia II (Jaeger et al., 1973) being the oldest known to date. The specimens from the Kechabta Formation are fragmentary and few in number, but appear to represent species more advanced than *Progonomys cathalai.* They are quite probably referable to the genus *Anthracomys* (Petter, 1968; Jaeger, 1975), showing some resemblance to *Anthracomys majori* as characterized by Missone (1969:83) and *Anthracomys miocaenicus* (Jaeger, 1975). Indeed, it is difficult to separate *Anthracomys* (Michaux, 1969:14) from *Paraethomys* (Jaeger, 1975:87). In both, stephanodonty is said to be moderately developed; the posterior cingulum (Z) is very reduced or absent on the upper and lower first molars; there is no anterior cusp (Sm) on M_1 and the cingular cusps of M_1 are reduced. In the original description of *Paraethomys filfilae* (Petter, 1968) the only comparisons made to a fossil murid were to the strongly stephanodont *Stephanomys donnezani.* In other discussions of both *Paraethomys* and *Anthracomys* (see Michaux, 1969; Missone, 1969; Jaeger, 1971, 1975) no comparisons between the two genera are made. It would seem that these two genera are congeneric, with *Anthracomys* having priority. Valid species would include:

Anthracomys majori (Schaub) 1938
Anthracomys filfilae (Petter) 1968
Anthracomys meini (Michaux) 1969
Anthracomys anomalus (De Bruijn et al.) 1970
Anthracomys miocaenicus (Jaeger et al.) 1975

We would exclude *A. ellenbergeri* from this genus, following Michaux (1969:11), who established the genus *Valerymys* for this species.

The Tunisian specimens are not sufficiently complete to warrant the naming of new taxa, and they are not assignable to any known species of *Anthracomys*. Two species are present, one (*Anthracomys* sp. B) considerably larger than the other (*Anthracomys* sp. A), but otherwise quite similar in occlusal morphology.

Anthracomys Schaub, 1938
***Anthracomys* sp. A**
Figs. 11, 12; Table 2

Referred specimens.—T-4080, RM^1; T-3808, RM^1; T-4212, RM$_2$.

Locality.—Voie Ferrée; Turolian.

Description.—The enamel has been lost along the labial cusps and on T2 of M^1. T1 is set well back of T2 with its anterior border in line with the posterior border of T3. T1 and T4 are of equal size and there is a well defined though narrow crest from T1 to T4. A crest was probably also present from T3 to T6. T4 and T6 lie behind T5. There is no T7 and T9 is small. The stephanodont crest T4 to T8 and T6 to T9 are present. There are no cingular cusps on M^1, and Z, if present was quite small. M^2 has T1 much larger than T3 and set further posteriorly than T3. There are no crests from T1 to T4 or T3 to T6. Crests from T4 to T8 and T6 to T9 are prominent. Z is very small.

***Anthracomys* sp. B**
Figs. 13-16; Table 2

Referred specimens.—UCM-34887, RM^1–RM^3; T-4211, LM^1; UCM-34886, RM^2; T-4242, LM^3; T-4210, RM$_1$; T-4241, RM$_1$; UCM-34888, LM$_1$; T-4208, LM$_2$.

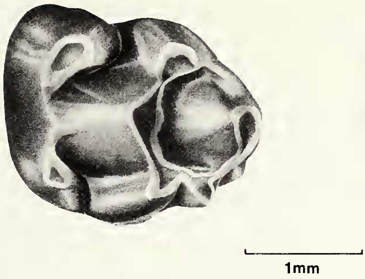
Locality.—Voie Ferrée; Turolian

Description.—The maxillary fragment with M^1–M^3 is badly cracked as are the teeth. The cusps on the upper molars are large and rounded. There does not appear to be any overlap of M^2 by M^1. T1 is set behind T3 but not as markedly as in the smaller form. There are no T1 to T4 or T3 to T6 crests, but there are thin crests from T4 to T8 and T6 to T9. T9 is much larger than it is in the smaller *Anthracomys* sp. A. Z is present on M^1 as a small spur off the posterolabial corner to T8. On M^2, T1 is much larger than T3. T4 to T8 and T6 to T9 crests are present. Z is quite small.

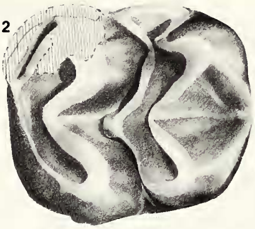
On M$_1$ there is no trace of either Sm or Z. The principal cusps are slightly alternate with S1 larger than Sv and set somewhat forward of it. Posterointernal crests from S1 and Sv join in the midline of the tooth halfway below the cusp apex and, somewhat lower, these are in turn joined by anterointernally directed crests from Epd and Eod. End and Td also join about halfway down their medial slopes. There is no eocrista. There are labial angular cusps at the base of Eod and Td.

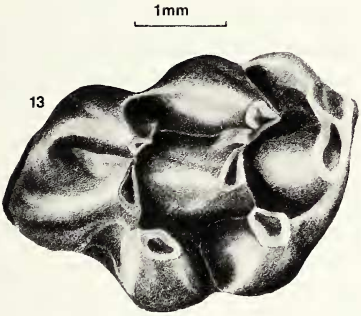
Discussion.—Both of these species display a mosaic of what are considered by Missone (1969) to be primitive characters. The posterior position of T1 and T4, the relatively short M^1 in relation to M^2, the lack of M^1–M^2 overlap, and the small number of cingular cusps on M$_1$ are probably primitive traits. In contrast, the small T9, small upper Z

11



12





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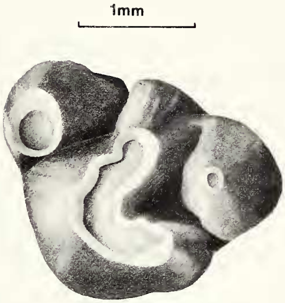
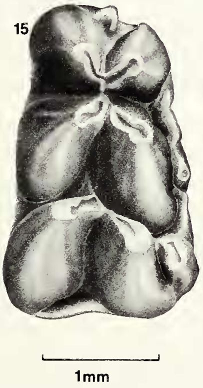


15



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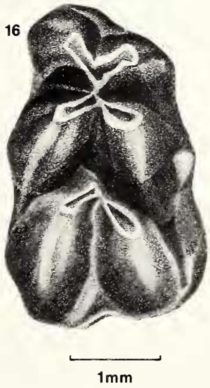

Figs. 11, 12.—*Anthracomys* sp. A. 11) T-3808, right M^2. 12) T-4212, right M_2.
Figs. 13–16.—*Anthracomys* sp. B. 13) T-4211, left M^1. 14) T-4242, left M^3. 15) T-4241, right M_1. 16) T-4210, right M_1.

and absence of Sm and Z on M_1 are considered to be advanced characters. The lower Z is present in both *Progonomys* and *Parapodemus* but absent in *Anthracomys*. There is no stephanodonty in the former two genera, whereas there is some indication of this condition in *Anthracomys*. The upper Z is small in all three genera.

Anthracomys quite probably evolved from *Progonomys,* involving loss of Sm, reduction of upper Z, loss of lower Z, and a trend towards stephanodonty with T3–T6, T6–T9, and T4–T8 crests. Primitive characters of *Progonomys* retained in *Anthracomys* include the cingulum with only two small cusps on M_1, the posterior position of T1 and T4, and the still relatively short M^1_1.

Anthracomys sp. A is somewhat smaller than *A. miocaenicus* from Morocco, but this may not be significant considering that only two teeth are known from Tunisia. The larger species, *Anthracomys* sp. B, is perhaps about the same size as *A. filfilae*. There is too little material of both species to make any definitive specific assignments.

SUMMARY OF KECHABTA FORMATION LOCALITIES AND FAUNAS

Oued Mellegue, near base of unit
  Family Equidae
    Hipparion sp. (Biely et al., 1974)
Oued Mellegue (Voie Ferrée), near top of unit
  Family Soricidae
    Soricid indet.
  Family Sciuridae
    Atlantoxerus sp.
  Family Muridae
    Anthracomys sp. A.
    Anthracomys sp. B.
  Family Ochotonidae
    Prolagus sp.
Araguib Kammra C
  Family Cricetidae
    Myocricetodon sp. cf. *M. seboui*
Araguib Kammra B
  Family Sciuridae
    Atlantoxerus sp.
MDM Locality, Sidi Ounis, near Zag et Tir
  Family Erinaceidae
    Schizogalerix ?moedlingensis
  Family Cricetidae
    Zramys jaegeri, new species

Family Sciuridae
Atlantoxerus sp.

Except for *Atlantoxerus* sp., there are no species common to any of the localities, making correlations difficult. On physical stratigraphic criteria, the Araguib Kammra and MDM localities should be the youngest, as the former is near the contact with the Oued bel Khedim Formation and the latter is below the freshwater limestones that are presumed to be correlative with the Oued bel Khedim (Burollet, 1956). The Voie Ferrée locality occurs below an angular unconformity, and at that locality the Oued bel Khedim, if it was ever present, is presumed to have been lost by erosion.

The only biostratigraphically useful species from the Araguib Kammra is *Myocricetodon* sp. cf. *M. seboui* which could range from mid-Vallesian to mid-Turolian (Jaeger, 1977*b*). Although *Zramys jaegeri* has not been reported from elsewhere, the stage of evolution of the species compared to that of other species of *Zramys,* indicates that it may be Turolian, possibly as young as mid-Turolian. The *Anthracomys* from Voie Ferrée is comparable with the *Anthracomys* from Amama 2 and Khendek el Ouach (Jaeger, 1977*b*) and therefore may also be mid-Turolian, as is the species of *Schizogalerix.*

Jaeger (1977*b*) reported that his locality at Djebel Semmene was probably mid-Vallesian, a conclusion which seems highly probable. As the lower part of the Kechabta Formation may well intertongue with the upper part of the Hakima Formation (Biely et al., 1974), the range of mid-Vallesian to mid-Turolian for the entire Kechabta Formation is reasonable.

ACKNOWLEDGMENTS

We thank Robert W. Wilson for helpful discussions, and Nancy J. Perkins for the illustrations. This effort has been funded in large part by the Foreign Currency program of the Smithsonian Institution, with subsidiary funding by the University of Colorado, Carnegie Museum of Natural History, and Texas Tech University.

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